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Powdery Mildew Fungus *Oidium lycopersici* Infected-Tomato Plants Attracts the Non-Vector Greenhouse Whitefly, *Trialeurodes vaporariorum*, but Seems Impair Their Development

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Abstract: The mechanism underlying the mediation of the behavior and fitness of non-vector herbivores by fungal pathogen-infected host plants is still unclear. In this study, we experimentally assessed the effects of tomato (*Lycopersicon esculentum* L.) plant infection status on non-vector herbivores using tomato powdery mildew disease fungus (*Oidium lycopersici*) and the greenhouse whitefly *Trialeurodes vaporariorum* as a model multitrophic plant-pathogen, non-vector herbivore interaction. In behavioral bioassays, powdery mildew-infected plants (**PM**) and plants damaged by combined attack of powdery mildew and whiteflies (**PMWF**) attracted significantly more whiteflies (32.6% and 58.1% for **PM** and **PMWF**, respectively) than control (**Con**) plants (16.5%) or plants damaged only by whiteflies (**WF**) (24.2%). Whiteflies feeding on **PM** or **PMWF** plants secreted almost twice as much honeydew as on the **Con** or **WF** plants. This indicated that whiteflies fed more on diseased plants than healthy plants. However, the preferences and increased feeding did not increase the fitness and immature growth of *T. vaporariorum*, but significantly prolonged their immature developmental durations, compared with those of whiteflies that developed on **Con** plants or **WF** plants. The results showed that powdery mildew infestation attracted more whiteflies but reduced their development and fitness.

Keywords: *Trialeurodes vaporariorum*; behavioral preference; fitness performance; *Oidium lycopersici*; plant pathogen; Y-tube olfactometer; multitrophic interactions

1. Introduction

Agricultural crops face serious threats from insect herbivores and plant diseases which cause severe qualitative and quantitative damage to crops. Overall, plants are threatened by insect herbivores and phytopathogens either solely, simultaneously or sequentially, and due to these biotic factors, the production of primary metabolites fluctuates substantially;

thus, phytohormones of plant resistance are stimulated [1–3]. Therefore, infection by phytopathogens disturbs the chemical composition of plants, and the host plant becomes a favorite for insect herbivores and vice versa [4,5].

The fungal pathogens produce a large number of secondary metabolites, which have insecticidal properties, e.g., bassianolide, beauverolides, beauvericins, isaridins and destruxin [6], and these fungal metabolites can play an important role in the modification of primary and secondary plant metabolite profiles [7–9]. After infection by phytopathogens, the host plant attracts more or repels insect pests. Pathogenic infection leads to chemical profile modifications in the host plant and may affect the preference and performance of insect herbivores. Therefore, this modification in the host plant could be beneficial for or detrimental to various insect herbivores [5,10,11], since the impact of plant response against various insect pests varies with the co-infecting phytopathogens [12]. Likewise, Raman and Suryanarayanan [13] also reported that these chemical plant responses regulate the attraction or deterrence of insect pests after fungal infection. However, the resistance of pathogen-infected plants against insect pests could vary according to their mode of feeding. For example, plants infected with powdery mildew (PM) show differences in attractiveness between chewing and sap-sucking insect herbivores [14]. This finding was also confirmed by Stephanie et al. [15], who reported that the density of sap-sucking insects was greater on fungal-infected plants than that of chewing insect pests. Desneux et al. [16] and Li et al. [17] explained ecological relationships among host plants, insect pests, and phytopathogens, and categorized these responses into three types (positive, negative, and/or neutral). The consequences of such tripartite interactions may depend on some conditions: (i) plant resistance to or tolerance of phytopathogens and insect pests, (ii) species biology, (iii) abiotic stresses and (iv) the timing and scale of interactions [18]. Such interactions need further investigations to explore the impact of phytopathogens on plants and insect herbivores.

Oidium lycopersici Cook & Massee, the main agent of powdery mildew, is a pathogen commonly encountered since it was first recorded in Europe in the 1980s [19,20]. This plant disease is often accompanied by the simultaneous infestation of the plants by an important insect pest, the greenhouse whitefly *Trialeurodes vaporariorum* (Westw.) (Hemiptera: Aleyrodidae), which is one of the most destructive pests of vegetables in the world, particularly in the greenhouse [21]. Powdery mildew is a biotrophic pathogen [19]; thus, differences in tomato–powdery mildew–whitefly tripartite interactions are different from those of the plant–necrotrophic pathogens–chewing insects’ tripartite interactions, and the causes of these differences are unknown. The understanding of these tripartite interactions would aid in the development of more effective management strategies against whitefly, to evaluate the effects of PM infection of tomato plants, with or without whitefly infestation on feeding preference and performance of *T. vaporariorum*, under greenhouse conditions.

2. Materials and Methods

2.1. Plants, Pathogens, and Insects

Seeds of tomato (*Lycopersicon esculentum* L.) (Karst. ex Farw. 9) were sown in pots (2 L) with standard soil (Fruhstorfer Erde, type P) in a growth chamber, watered regularly, and fertilized twice a week with 70 mL commercial fertilizer (Hakaphos Blau, COMPO GmbH Co. KG, Münster, Germany: 3 g/L, 15% N, 10% P₂O₅, 15% K₂O, 2% MgO, 0.01% B, 0.02% Cu, 0.05% Fe, 0.05% Mn, 0.001% Mo and 0.015% Zn). After getting two leaves, plants were transferred to a glasshouse and maintained under natural light (23 ± 2 °C).

Powdery mildew, *O. lycopersici* (obtained from Entomological Section, Georg-August-University, Goettingen, Germany during 2020) was cultivated on the tomato plants (having 5–7 leaves) in a cage (1 × 1 × 1 m), 70 ± 5 R.H and 23 ± 2 °C. As the white powder of the conidia spores grew, the infected leaves with powder were cut with a razor and were used for inoculation. Plants were placed inside a clear plastic cage in the greenhouse (16-h-light/8-h-dark cycle). At eight days post-inoculation, a leaf disc was taken from leaf 2 with a cork borer and placed in a tube containing 0.5 ML of 0.01% (v/v) Tween 20 solution. This was vortexed, and three 2-μL drops were removed. The spores of the leaf

were counted using a haemocytometer, and the spore concentrations (spores per mm² of the leaf) were calculated.

Male and female adults of greenhouse whitefly, *T. vaporariorum* were collected from tomato plant of greenhouse and reared on tobacco (*Nicotiana tabacum* cv. Xanthi nc) plant in cages at 70 ± 5% RH and 22 ± 1 °C, light 14:10 h L: D for six months prior to experiments.

2.2. Inoculations and Plant Treatments

Tomato plants (up to the four-leaf-stage, grown in the glasshouse) were randomly selected for each treatment. The spores of four leaf discs, taken from infected leaves with powdery mildew, were wiped onto the four lateral leaflets of three leaves. The inoculated concentration of each plant was 4 × 10⁵ spores/mm². Control plants received no fungal treatment, and the infection rate was recorded before bioassays. All plants were kept in laboratory cages (2 × 1.5 × 1.5 m) until used in the experiments, at 23 ± 2 °C and 70 ± 5% RH.

Four-leaf-stage tomato plants were subjected to the following treatments: inoculated with powdery mildew from 3 d (three days post-inoculation, dpi) (abbreviated in the following: **PM**); infested with 50 adult whiteflies (female: male = 25:25, one day after emergence) for 24 h (**WF**); inoculated with powdery mildew 3 dpi, and after that, infested with whiteflies for 24 h (**PMWF**). The control plant had no treatment (**Con**). The pots and the soil were wrapped in aluminium foil (Greenwich, CT, USA).

2.3. Behavioral Bioassays

We investigated the short-range olfactory response of whitefly adults to **PM**, **WF**, **PMWF**, and **Con** plants as described above and compared the attractiveness of the volatiles emitted from the four treatment plants (**PM**, **WF**, **PMWF**, and **Con**) in a dual-choice-bioassay consisting of an all-glass Y-tube olfactometer (Bürkle GmbH, Bad Bellingen, Germany). The olfactometer setup consisted of a Y-shaped glass tube (base tube 13 cm long; Y-arms 5 cm; internal tube diameter 18 mm). As an odor chamber, we used a glass jar (Vakuumfest, 42 cm high, 38 cm in diameter) consisting of two parts with a ground glass joint. The odor chamber contained a treated plant. A scoreline was drawn on the two arms of the olfactometer at 4 cm from the joint. With air pressure, airflow was generated through an active charcoal filter for purification and then passed through a humidifier bottle. The humidified airflow was divided in two, and each sub-flow was led through an odor container. Subsequently, the two odor flows were led through the two arms of the Y-tube olfactometer. The airflow through each olfactometer arm was 10 L/h and was checked with a flowmeter. For the bioassay, individual *T. vaporariorum* virgin females (one day after emergence) were released at the open end of the common arm of the Y-tube. The experiment was done at 23 ± 2 °C and 70 ± 5% RH in a white box with an artificial light source consisting of a single 35-W fluorescent tube placed above the arms of the Y-tube. A choice was recorded when the adults crossed the scoreline within 5 min from release and stayed in the portion of the arm behind the scoreline for at least 1 min. The connections of the odor source container to the olfactometer arms were exchanged after testing five whiteflies to remove any asymmetrical bias of the set-up. The olfactometer tube was washed with alcohol and dried, and the two plants were replaced by new ones after testing ten females. Fifty replicates were carried out per dual-choice treatment.

2.4. Herbivore Fitness Performance

Twenty-five whitefly females and 25 males were paired and mated, then introduced into a cage containing six plants (5–6 leaves stage) for each treatment (**PM**, **WF**, **PMWF**, and **Con**) as described above separately for 24 h. After ovipositing (24 h post-exposure), the whiteflies were removed using an aspirator and the eggs laid were recorded. The development time of eggs, larvae, pupae and adults were recorded. The experimental design was a randomized complete block design with four treatments and the trials were replicated six times.

For determining the impact of the powdery mildew infection on honeydew production of whiteflies, the honeydew was collected by a modified method following previous studies [22,23]. Briefly, clip cages were prepared by placing an aluminium foil of known weight on the bottom of a clip cage. Ten newly emerged whiteflies (female: male = 5:5) were introduced into these clip cages and confined to the underside of the leaf to facilitate honeydew collection. After 24 h, the weight of the secreted honeydew was assessed by weighing the aluminium foil, measured using the thousandth (0.001) Balance (model Micro MC5/SC2, Sartorius, Goettingen, Germany). The volume of honeydew was measured using the bromocresol green technique [24]. In this experiment, a filter paper treated with bromocresol green was introduced into the clip-cage bottom instead of the aluminium foil. After 24 h, the filter papers were harvested and the blue spots on the filter paper were measured. The experimental design was a randomized complete block design with four treatments, and the experiments were replicated six times.

2.5. Statistical Analysis

The rate of infection after inoculating the plants with the pathogen was calculated using the following formula:

$$\text{Infection rate (\%)} = \frac{\text{No. of infected plants}}{\text{No. of inoculated plants}} \times 100 \quad (1)$$

Behavioral bioassays data were analyzed for preference (percentage of whiteflies making a choice, i.e., selecting either an odor of the treatments or the controls and those that made no choice were excluded from the analyses). The Bonferroni paired *t*-test was used with Systat 12 for Windows for possible differences between treatments and control. Analysis of performance parameter (honeydew production, developmental time) data were based on six replications per treatment, where the data were subjected to analysis of variance using Systat 12 for Windows. Means were compared using Duncan's multiple range test (DMRT) at a significance level of 5%.

3. Results

3.1. Behavioral Bioassays

The infection rate of the tomato plants ranged from 98.2% to 100%. The percentage of behavioral preference responses of whiteflies under different treatments varied between 49.20% and 90.67%. **Con** plants revealed no significant difference between the left arm and right arm ($t = 0.101$, $n_1 = 50$, $n_2 = 50$, $p = 0.925$), indicating that no bias existed in the experimental setup. The adult whiteflies significantly preferred **Con** plants as compared to clear air (CA) ($50 \pm 5.54\%$ vs. $21.67 \pm 7.83\%$, $p = 0.002$; Figure 1), indicating that adults of *T. vaporariorum* are able to locate these host plants.

Although no significant differences in attractiveness of *T. vaporariorum* were detected between **PMWF** and **Con** plants ($38.69 \pm 6.24\%$ vs. $34.48 \pm 6.69\%$, $t = 0.363$, $n_1 = 50$, $n_2 = 50$, $p = 0.731$); **PMWF** and **PM** plants ($40.00 \pm 8.38\%$ vs. $22.50 \pm 8.54\%$, $t = 0.812$, $n_1 = 50$, $n_2 = 50$, $p = 0.476$), **WF** and **PM** plants ($31.88\% \pm 3.55\%$ vs. $47.26\% \pm 10.36\%$, $t = -1.331$, $n_1 = 50$, $n_2 = 50$, $p = 0.254$), statistically significant differences in the attractiveness of *T. vaporariorum* were observed between **PM** and **Con** plants and **PMWF** and **WF** plants.

Powdery-mildew-inoculated plants significantly attracted more whiteflies than **Con** plants (Figure 1; $32.62 \pm 4.26\%$ vs. $16.50 \pm 5.32\%$, $p = 0.02$), while **WF** plants were significantly less attractive to whiteflies as compared to **Con** plants ($20.00 \pm 5.16\%$ vs. $58.33 \pm 4.01\%$, $p < 0.001$; Figure 1). Whiteflies significantly preferred **PMWF** plants (the whitefly-damaged + fungal-inoculated plants), compared to **WF** plants (whitefly-only damaged plants) ($58.05 \pm 1.24\%$ vs. $34.16 \pm 4.54\%$, $t = -5.401$, $n_1 = 50$, $n_2 = 50$, $p = 0.003$).

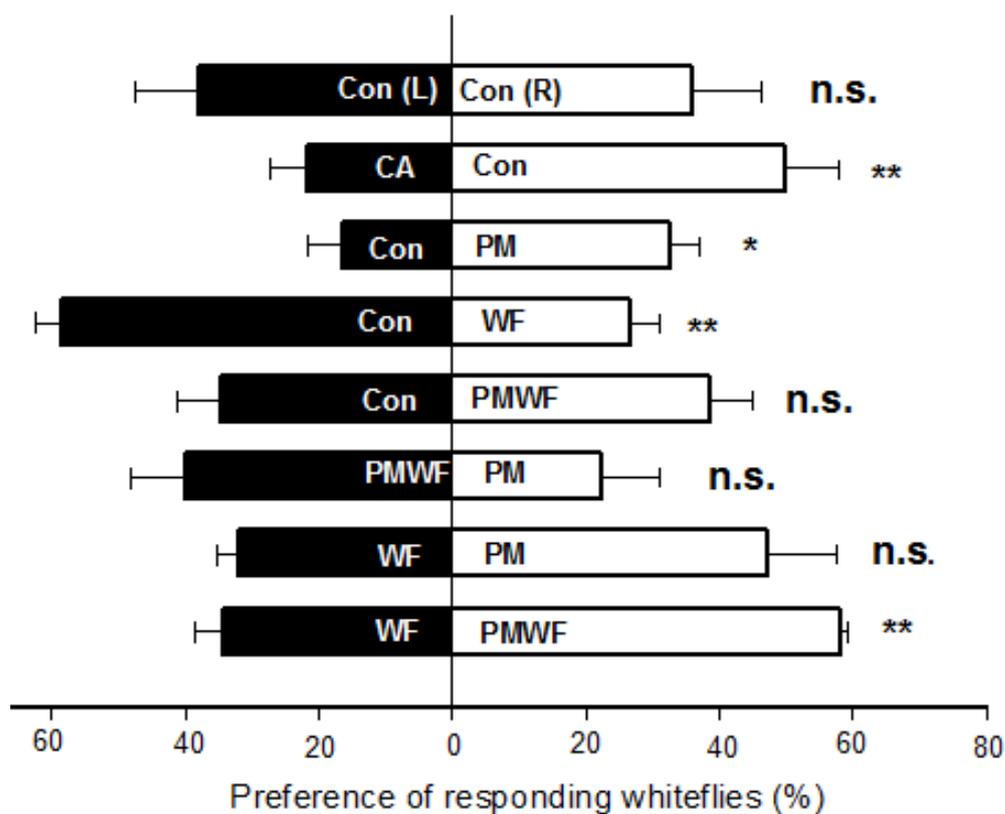


Figure 1. Preference of *T. vaporariorum* for the four treated plants (CA, Clear Air; Con, Controls; PM, powdery mildew plants three days after inoculation; PMWF, powdery mildew plants three days after inoculation and infested by whiteflies for 24 h; WF, healthy plants infested by whiteflies for 24 h). There were 50 replicates for each treatment. The bars indicate the percentage of response/preference in the Y-tube olfactometer test (* $p < 0.05$ and ** $p < 0.01$ according to the Bonferroni paired t -test) ($n = 50$). Error bars represent standard errors and asterisks and n.s. indicates the significance level with n.s. = not significant.

3.2. Herbivore Fitness Performance

When feeding on PM or PMWF plants, whiteflies secreted a significantly greater volume of honeydew ($F_{3,20} = 19.15$, $p < 0.001$), but developed more slowly. The results showed significant differences among treatments for eggs laid ($F_{3,20} = 6.82$, $p = 0.002$); larvae ($F_{3,20} = 99.79$, $p < 0.001$); and pupae ($F_{3,20} = 27.66$, $p < 0.001$) when using the post-hoc separation of means with Duncan's multiple range test ($p < 0.05$). The average developmental time at egg stage was 6 d on Con plants versus 7 d on PM plants, 6.8 d on PMWF, and 6 d on WF. In addition, the average developmental time for the larval stage was 15.8 d on Con, versus 17 d on PM, 16.8 d on PMWF, and 16 d on WF. The average developmental time for the pupal stage was 3.7 d on Con, versus 4 d on PM, 3.8 d on PMWF, and 3.8 d on WF (Figure 2). Whiteflies feeding on PM or PMWF plants secreted nearly twice more honeydew as those feeding on Con plants or WF plants.

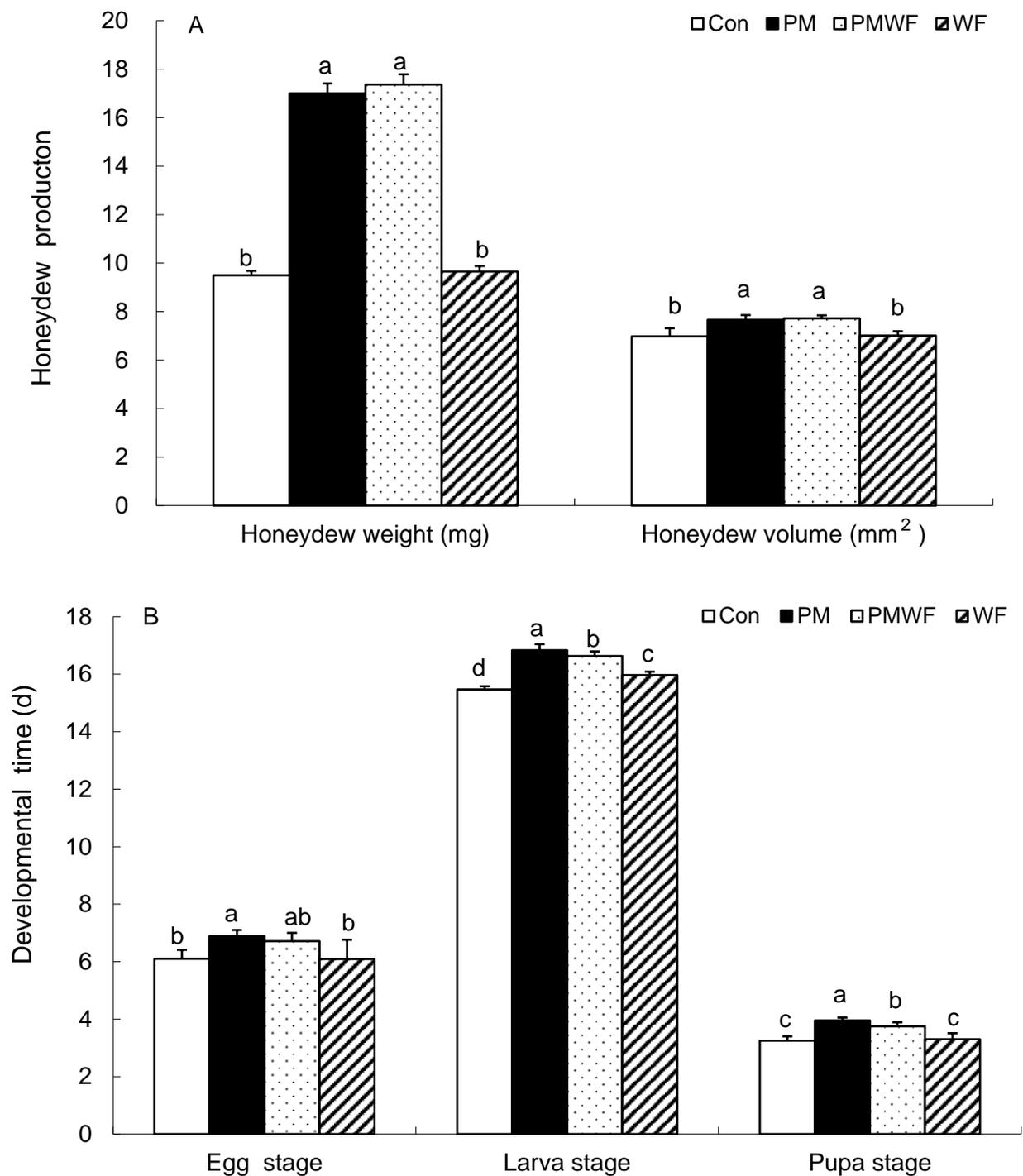


Figure 2. Effects of powdery mildew infections on the performance of *T. vaporariorum*: (A) honeydew production; (B) developmental time. There were six replicates for each treatment, $n = 30$ for each replicate of developmental time trial; $n = 10$ for each replicate of honeydew production trial. Bars (mean \pm SD) followed by the same letters are not significantly different [$p > 0.05$; post hoc Duncan's multiple range test (DMRT) (SPSS Inc., 2000)].

4. Discussion

The effects of fungal infection on insect feeding preference and their performance on host plants vary widely. It may be beneficial or detrimental, or even more complex, depending on the species involved [25]. Inoculation of tomato plants with powdery mildew fungus, *O. lycopersici* attracted significantly more whitefly adults, for feeding or oviposition.

The attraction of phytophagous insects to the host plants involves both olfactory and visual cues. When visual cues are not available, the olfactory cues are powerful and may be the most important stimuli during this phase of host searching and location [7,26–28]. Our olfactometer experiment results demonstrated that the attraction of whiteflies for feeding or oviposition relied on the olfactory cues. In addition, adult whiteflies could discriminate between infected plants and showed a preference for feeding, as indicated by the increase in honeydew production.

Our results are similar to the findings of Moran [29], who found that the preference of spotted cucumber beetle, *Diabrotica undecimpunctata howardi* (Coleoptera: Chrysomelidae), was higher for leaf disks from partially necrotic local cucumber leaves of plants inoculated with *Cladosporium cucumerinum*. Likewise, whiteflies preferred the **PM**-infected over **Con** plants, with a preference for **PMWF** plants over **WF**-infected plants. However, the preferences and increased feeding did not benefit the growth of *T. vaporariorum*. This phenomenon has also been reported in several cases dealing with plant-pathogen-herbivore interactions [29,30]. For instance, Li et al. [17] stated that insect feeding acts as an indicator of the ecological cross-effects of infection; however, interactions between the insect and plant pathogenic fungus could have either a positive or negative impact on each other. Likewise, previous studies reported that a decline in the growth of immature forms was detected in whitefly, while greater production of honeydew was observed from whitefly feeding on fungal-diseased plants [23,31].

On the other hand, findings of Ajayi and Dewar [32] as well as of Fiebig et al. [33] are contradictory to our results, as they found that wheat aphids produced less honeydew on viral-infected (barley yellow dwarf virus, BYDV) wheat leaves compared to healthy wheat leaves. In the current study, we found that whiteflies secreted significantly more honeydew when fed on **PM**-infected plants; therefore, it is hypothesized that whiteflies feed more on diseased plants than on healthy plants.

Plant volatile emissions can be produced by the infection of plant pathogens, which insects may exploit for locating or discriminating between host plants. Our results are consistent with previous reports, which support our current hypothesis [34–36]. The olfactometer test in our current study indicated that the effect on the preference of adult whiteflies was caused by the changes in the qualities and quantities of volatile emissions from the powdery mildew-diseased tomato plants [34,37]. We previously reported that both qualities and quantities of volatile compounds differed to a large extent [38]. Plants significantly increased volatile emission after being attacked by whiteflies (275.3 mol h^{-1}) or inoculated by powdery mildew ($267.58 \text{ mol h}^{-1}$); however, plants significantly reduced volatile emissions in **PMWF** co-existing systems (80.58 mol h^{-1}). Several previous studies have revealed that volatile chemicals produced by plant responses to pathogen infection affect phytophagous insects' feeding or oviposition preferences [35,36].

5. Conclusions

The current study revealed that there was a significantly greater attraction of greenhouse whiteflies to **PM** plants, compared to **Con** plants. On the other hand, *T. vaporariorum* development was prolonged on **PM** plants, compared to **Con** plants. However, honeydew production was higher on diseased (**PM**, **PMWF**) plants than on **Con** plants. Detailed work is needed to explore the changes in the metabolic chemicals (especially antioxidant enzymes) of the infected plants by the plant pathogen *O. lycopersici* and the role of this plant pathogenic infection in the plant-induced resistance, focusing on the P450 system (CYP genes). However, our results demonstrate that host-plant infection by a biotrophic fungal pathogen attracts more non-vector herbivores but impairs/hampers their development. Diseased host plants may significantly impact the outcome of biological control of *T. vaporariorum*, especially under greenhouse conditions. Further studies are warranted to explore the major chemical compounds involved in the behavior and herbivory of *T. vaporariorum* for the development of effective and sustainable management approaches against the pest.

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